DESCRIPTION AND BIOLOGY OF A NEW SPECIES OF PELAGIC PENAEID SHRIMP, *BENTHEOGENNEMA BURKENROADI*, FROM THE NORTHEASTERN PACIFIC¹

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ABSTRACT

The new species of pelagic penaeid shrimp lacks the richly plumose arthrobranch described for the genus and has a single pair of terminal spines on the telson. It is found mainly in transitional water of the North Pacific between 500 and 1,000 m by day and 150 and 1,000 m at night. Examination of testes and ovaries, and the structures of the petasma and thelycum, indicates a 4-5 mospawning season and an equal male to female sex ratio. Generation time was estimated to be 2 yr.

This paper describes the systematics and biology of a new species of pelagic penaeid shrimp of the genus *Bentheogennema*. Since 1961, studies of the fauna and ecology of the mesopelagic waters off the coast of Oregon have been conducted by members of the School of Oceanography, Oregon State University. Several unusual species of macrurous decapod Crustacea have been obtained. The discovery and identification of this new species of *Bentheogennema* was by Carl Forss, who entrusted his material to the authors. Subsequent sampling with mid-water trawls has provided detailed information on the distribution and biology of this shrimp, as well as abundant material for taxonomic description.

METHODS AND MATERIALS

Material for the zoogeographic distribution was collected in Isaacs-Kidd Mid-water Trawls (IKMT) from the research vessels Yaquina, Endeavor, John R. Manning, and Hugh M. Smith in the northeastern Pacific, normally within 320 m of the surface (Wasmer 1972). Information on vertical distribution, reproductive biology, and growth of this species was obtained from samples taken on five cruises aboard RV Yaquina at a single sampling station 65 nautical miles (120 km) off the central Oregon coast (NH 65-lat. 44°35'N, long. 125°25′W) in 1972-73. Samples at this station were taken both day and night, using an 8-foot IKMT with a five net opening-closing cod end section similar to the one described by Pearcy and Mesecar (1971).

All samples were preserved at sea in 10% buffered Formalin.⁴ The samples were later sorted, identified, sexed when possible, and measured. Carapace length (measured from the postorbital margin to the median posterior edge of the carapace) was used as an indication of size. All figures were drawn with the aid of a camera lucida.

In males, sexual maturity was based on three characteristics: 1) petasmata joined; 2) welldeveloped accessory lobe on anterior surface of the petasma; 3) and dilated vas deferens with large terminal ampoule (indicative of developed spermatophore) at the base of the fifth pereiopod. The combined characteristics of fully developed thelycum and the posterior lateral lobe of the ovary swollen with eggs at the base of the fifth pereiopod were used as signs of sexual maturity in females. Estimates of growth are presented from analysis of length-frequency data.

Section Penaeidea Family Penaeidae Bate Subfamily Aristaeinae Alcock Series Benthesicymae Bouvier Bentheogennema burkenroadi n. sp.

Types.-Holotype (USNM 150835), male, carapace length (c.l.) 18 mm, from Station lat.

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51°26'N and long. 138°28'W, Mid-water Trawl No. 857 (MT 857); Allotype (USNM 150836), female, 14.5 mm c.l., station Newport Hydrographic Line 65 nautical miles (120 km) offshore (NH 65), MT 2130; Paratypes: 1 male (USNM 150837), 15 mm c.l., from NH 265, MT604; 2 males (USNM 150838), 8 and 6.5 mm c.l., NH 65, MT 2088; 1 male (USNM 150839), 14 mm c.l., NH 65, MT 2131; 1 male (USNM 150840), 13.5 mm c.l., NH 65, MT 2130; 4 females (USNM 150841), 14.5, 14, 10, 18 mm c.l., NH 65, MT 2130; 4 males (USNM 150842), 12.5 13.0, 13.2, 17.5 mm c.l., NH 65, MT 2130; 1 male (USNM 150843), 9.0 mm c.l., NH 50, MT 570; 1 male (USNM 150844), 9.5 mm c.l., lat. 40°28', long. 133°46', MT 613; 3 females (USNM 150845), 13.3, 14.0, 15 mm c.l., NH 65, MT 2121 Net #5; 1 female (USNM 150846), 20.0 mm c.l., NH 65, MT 2133 Net #1; 2 females (USNM 150847), 7 and 10 mm c.l., NH 65, MT 2070 Net #5; 2 males, 1 female (BMNH 1975:10), 14.2, 16.4, 13.2 mm c.l., NH 65, MT 2175 Net #5; 1 female (BMNH 1975:10), 15.7 mm c.l., NH 65, MT 2178 Net #4; 1 female (BMNH 1975:10), 12.6 mm c.l., NH 65, MT 2302 Net #4; 1 male (BMNH 1975:10), 11.5 mm c.l., NH 65, MT 2301 Net #1. Other, nonparatype, material deposited at Los Angeles County Museum; Fisheries Research Board of Canada Biological Station, Nanaimo, British Columbia; and School of Oceanography, Oregon State University, Corvallis, Oreg.

Diagnosis.-Benthesicymae with podobranch on second maxilliped to third pereiopod inclusive; first maxilliped with single rudimentary arthrobranch; only sixth abdominal somite with middorsal carina; telson distally truncate, usually with single pair of mobile terminal lateral spinules. Accessory lobe of petasma characterized by large upturned terminal hook. Plate of thelycum on sixth thoracic sternite triangular and elevated, projecting ventrally in strong ridge; plate on eighth thoracic sternite pentagonal with anteriormost angle concave and anterolateral margins bearing spines.

Description.-Rostrum extending to level of eye tubercle, well elevated above middorsal carina of carapace (Figure 1). Margin between rostral tip (apex) and dorsal spine with usual setal fringe (although broken in type). Middorsal carina of carapace bearing minute tubercle posterior to



FIGURE 1.-Mature female Bentheogennema burkenroadi n. sp. illustrating the (a) anterior and (b) posterolateral lobes of the ovary.

dorsal spine; carina absent between well-defined cervical and postercervical sulci and on posteriormost portion of the carapace. Mid-lateral longitudinal carina consisting of strong antennal carina continuous with hepatic and branchial carinae. Branchiostegal spine small and branchiostegal carina distinct; hepatic sulci continuous from branchiostegal spine towards lower margin of carapace; post-hepatic carina orientated dorsoventrally from longitudinal hepatic carina toward inferior margin of carapace. Antennal angle obtuse and infra-antennal angle acute (Figure 2a).

Only sixth abdominal somite with middorsal carina; second through fifth abdominal somites with weak lateral ridges in approximately dorsoventral position extending from mid-lateral to ventrolateral edge of the pleuron. Fourth, fifth, and sixth abdominal somites with prominent, roughly transversal, lateral ridges which together form "half moon" area (Figure 1). Fourth and fifth abdominal somites bearing small mid-lateral tooth on posterior margins.

Antennal flagellum (Figure 1) similar to Gennadas (Foxton 1969), having proximal and distal sections divided by short series of annuli forming kink in flagellum; proximal section rigid, bearing scattered short nonplumose setae; distal section bearing paired arched plumose setae with small plumose setae perpendicular to flagellum at irregular intervals between bases of some arched pairs. Second element of antennular peduncle, along dorsal midline, 0.7 ultimate element (Figure 2b). Antennal scale (Figure 2c) little less than 3 times as long as greatest width; distinct spine (outer margin of scale), slightly convex, terminal end free, not extending beyond narrow apex of blade.

Mandible (Figure 2d) with two segmented palp; palp thickly covered with setae on medial and lateral margins, distal element not quite as long as widest portion of basal element. Endopod of first maxilla (Figure 2e) distally narrow, with tip rounded; proximal gnathobasic lacinia (endite of coxa) subequal in width to distal lacinia (endite of basis), both terminating in strong spines among setae fringe. Anterior lobe of proximal lacinia (endite of coxa) of second maxilla (Figure 2f) strongly constricted behind apex, not broader than posterior lobe of distal lacinia (endite of basis); anterior lobe of distal lacinia very broad; endopod distally long and narrow, with two (sometimes three) curved spines at base of apical portion.

Endopod of first maxilliped (Figure 2g) reaching beyond endite of basis but falling short of exopod; endopod of four elements, third less than twice second; fourth extremely minute; first element bearing usual compliment of three curved spines on distomesial margin. Exopod bladelike, without constricted, segmented distal portion. Merus of second maxilliped (Figure 2h), including anterior prolongation, 1.9 times as long as wide; dactylus with single strong apical spine surrounded by medium and small spines back to proximal end of propodus; merus and carpus with numerous spines and setae; podobranch present. Third maxilliped (Figure 2i) reaching to, or beyond, middle of ultimate joint of antennal peduncle; ischium nearly 3 times as long as greatest width; merus usually twice as long as greatest width; carpus slightly longer than propodus; dactylus with long slender terminal spine; podobranch present.

Merus of first pereiopod (Figure 3a) 1.4 times length of carpus and 1.7 ischium; fingers slightly setose. In second pereiopod (Figure 3b), carpus 1.2 times length of propodus; merus 1.2 carpus and 1.5 propodus; chela with heavy tufts of bristles. Merus and carpus of third pereiopod (Figure 3c) of equal length, each twice ischium; fingers of chela similar to those of second pereiopod. Carpus and propodus of fourth pereiopod nearly equal, each approximating two-thirds of merus which is 2.4 times ischium. Propodus of fifth pereiopod subequal to carpus which is subequal to merus; ischium slightly more than one-third of merus.

Outer scale of appendix masculina (Figure 3d) longer than inner; proximal half of lateral margin expanding slightly then tapering toward base. Inner scale broadly rounded distally; spines on distomesial margin (few to many) long and thin, spines on distal margin smaller, stronger, and of uniform length.

Telson with single pair of mobile terminallateral spines (Figure 3e) fringed with setae on terminal and distal two-thirds of lateral margins (of the large number of specimens inspected, only two mature males had any indication of more than one pair of mobile spines (USNM 150839, 150840), each with two pair of mobile spines on terminal edge of telson). No mobile nonterminal-lateral spines present on telson. Lateral margins of lateral rami of uropods (Figure 3f) bearing spine at 0.78 total length. Mesial rami about 0.73 lateral rami.

Each half of petasma (Figure 3g, h), distally divided into three lobes (external, median, and in-



FIGURE 2.—*Bentheogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, carapace; b, antennular peduncle; c, antennal scale; d, mandible; e, first maxilla; f, second maxilla; g, first maxilliped; h, second maxilliped; i, third maxilliped. Scale equals 1 mm.

ternal (Balss 1927) which are equivalent to Burkenroad's (1936) distoventral, distolateral, and distomedian lobes). External lobe bipartite; lateral part elongate projection with minute terminal teethlike protuberances distally; mesial part curving inward with apex directed toward median lobe. Median lobe broadly rounded; subdistally, accessory lobe on anterior face of petasma, characterized by large upturned terminal hook (Figure 3g) with free margin attaching to base of

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FIGURE 3.—*Bentheogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, first pereiopod; b, second pereiopod; c, third pereiopod; d, appendix masculina; e, distal half of telson; f, uropod; g, anterior view of petasma (EL = external lobe, ML = median lobe, IL = internal lobe, AL = accessory lobe); h, posterior view of petasma; i, anterior view of petasma from young male (8.0 mm c.l.); j, anterior view of petasma from young male (9.0 mm c.l.); k, anterior view of petasma from young male (9.5 mm c.l.); I, thelycum of female (17 mm c.l.), arrow pointing to right sperm receptacle. Scale equals 1 mm.

median lobe, attachment area distinguishable to level of elongate projection of external lobe. Internal lobe undivided, bearing rigid hooks continuous with row of cincinnuni, holding two halves of petasma together. The accessory lobe develops early in the juvenile stage (Figure 3i, j, k) and together with characteristic spination of telson and presence of podobranchs behind second maxilliped, young of this species were discernable to a size of 6 mm c.l. (the smallest size captured).

Thelycum (Figure 31) with plate on eighth thoracic sternite pentagonal, with anteriormost angle concave, anterolateral margin bearing long spines (this plate exhibits greatest variation during growth, being more rectangular in young females, changing to the pentagonal shape of maturity but becoming almost bilobed in very large females). Plate of seventh thoracic sternite bearing three anterior directed projections; lateral pair, shortest, bearing short spines; center projection exhibits varying amount of concavity after maturity such that distolateral margins may appear as raised wings. Elevated plate on sixth thoracic sternite triangular and inverted "V" shaped, with apex pointing anteriorly; apex not reaching anterior limit of sternite. Sperm receptacles located toward lateral edges near bases of inverted V.

Coloration at time of capture varying from deep red over entire body to medium red on cephalothorax and lighter on abdomen. Black pigment fleck on distolateral edge of ocular peduncle just below corneal region (Figure 2a). Other small flecks of purple pigmentation often observed on carpus and propodus of third maxilliped and first and second pereiopods, on carpus of third pereiopod, and on ventral surface of abdominal somites just anterior to lateral edge of base of each pleopod.

Remarks.-Burkenroad (1936) proposed the genus Bentheogennema for those species of Gennadas Bate which possesses podobranchs on the second maxilliped to third pereiopods inclusive. Other generic characters he included were: arthrobranch of first maxilliped large and richly plumose; exopod of first maxilliped without a constricted, segmented distal portion; dorsal carina on sixth abdominal somite only; telson with truncated apex and more than a single pair of mobile lateral spinules.

As is often the case, the addition of a new

species changes the generic formula for that group. The new species is similar to *Gennadas* in the armature of the telson but more closely resembles *Bentheogennema* with podobranchs on the second maxilliped through third pereiopod. We agree with Kemp (1909) and Burkenroad (1936) that the presence of podobranchs, a primitive characteristic, is a more important generic trait than the number of pairs of spines on the telson.

We found that the two species of Bentheogennema-B. borealis (Rathbun) and B. burkenroadi n. sp.-from the Oregon coast lack the large, richly plumose arthrobranch on the first maxilliped that Burkenroad (1936) included as a generic characteristic. Both have small rudimentary arthrobranchs similar to Gennadas. We assume that Burkenroad (1936) did not have samples of B. borealis but included this arthrobranch structure as a generic characteristic from samples of B. intermedium (Bate) and B. pasithea (Man).

Although Tirmizi (1959) stated that the endopod of the first maxilliped is five-segmented in *Gennadas* and apparently only four-segmented in *Bentheogennema*, we have found that *Gennadas propinquus* Rathbun off the Oregon coast has a four-segmented endopod. Hence these characters are not reliable to distinguish these two genera.

Bentheogennema burkenroadi can be separated from B. borealis, B. intermedium, B. pasithea, and B. stephenseni (Burkenroad) by the armature of the telson, and the structures of the petasma and thelycum. The telson of B. burkenroadi typically possesses only a single pair of terminal-lateral spines, whereas the other members of this genus possess two or more pairs of lateral spines: B. borealis and B. stephenseni two pairs; B. pasithea three pairs; B. intermedium (as described by Tirmizi 1959) four pairs. The number of spines present on the telson should not be held as an invariable characteristic, there is undoubtedly a small percentage of variation as exemplified by the two males of B. burkenroadi (USNM 150839, 150840) which possess two pairs of terminal spines. It is possible that one of the two specimens of Gennadas calmani (Kemp) (synonymy: B. borealis), which Kemp (1909) illustrated with two pairs of terminal spines is also an example of such variation.

The petasma of this new species is unique and easily distinguishable from that of other members of the genus. The combined structures of the accessory lobe with its mode of attachment, its large size, and its terminal hook (present in mature individuals) and the shape of the bipartate external lobes make identification, even of the juvenile stages (Figure 3g-k), possible.

The thelycum differs from that seen in other species by the pentagonal shape of the plate on the eighth thoracic sternite and the elevated triangular plate on the sixth sternite (Figure 31).

We have named *B. burkenroadi* after Martin D. Burkenroad, whose work on Crustacea, especially the Penaeidae, is well known.

GEOGRAPHICAL AND VERTICAL DISTRIBUTION

Shrimps were examined from mid-water trawl collections taken over much of the North Pacific (Figure 4). Bentheogennema burkenroadi was found only in collections from the northeastern sectors (lat. 52-34°N and east of long. 142°W) (Wasmer 1972). Pearcy and Forss (1966, 1969) observed *B. burkenroadi* off the coast of Oregon, as close as 28 km to the northern end of the coast and occurring \geq 92 km off the central and south coast. Wasmer (1972) found the greatest concentration

in the Transitional Water Mass (Figure 5), with a few individuals occurring in the Pacific Subarctic and eastern North Pacific Central Water Masses. It is assumed to be a transitional species, although as is the case for many shrimps, it is not totally confined to a single physicochemically definited water mass (Wasmer 1972). Since *B. burkenroadi* is a deep mesopelagic species and most of the available geographical collections were from shallow depths, the known geographic range will undoubtedly be increased by more systematic deep trawls in the eastern Pacific.

This species was captured in opening-closing nets from the surface to 1,000-m depth. It apparently demonstrates a diel vertical migration. The depth distribution is, with few exceptions, below 500 m during the day and below 100 m at night (Table 1). Neither day nor night distributions are confined to a narrow depth stratum but are diffused in concentration over a broad range. The nocturnal migration into the upper waters appears to entail only a small segment of the population with the main concentration remaining at depth. Those migrating above 500 m included both sexes, though the immature shrimp (<11-mm



FIGURE 4.-Cruise tracks of the North Pacific from which shrimp were enumerated, indicating mid-water trawl stations (solid dots). *Bentheogennema burkenroadi* n. sp. was collected at stations where dot is encircled.



FIGURE 5.—Zoogeographical temperature-salinity (T-S) capture diagram for *Bentheogennema burkenroadi* n. sp. Relevant water masses in darkest bands; medium band in T-S envelope for the station 65 nautical miles off Newport, Oreg. (NH 65); single lines indicate T-S diagram for sampling stations other than NH 65 where this shrimp was captured.

males and <12-mm females) were not observed to migrate as high in the water column as adults. Vinogradov (1968) earlier stated that the intensity of diurnal migration of zooplankters increases with age, and migration may be absent in early stages of development, and our observations concur with this.

More shrimp were caught in nighttime than daytime tows. This may be explained by enhanced visual avoidance of the net during the day (Pearcy and Laurs 1966). However, the lack of obvious differences in size structure between day and night caught shrimp (Figure 6) argues against increased daytime avoidance, as larger more mobile animals should be preferentially sampled at night. Another explanation for the increased nighttime catch, as suggested for *Acanthephyra purpurea* Milne-Edwards and *Gennadas valens* (Smith) by Foxton (1970a, b), is migration up from below our maximum sampling depth of 1,000 m. Such a migration is indicated by the high concentrations between 600 and 1,000 m both day and

TABLE 1.-Seasonal diel vertical distribution to a depth of 1,000 m of mature males (\geq 11 mm c.l.), mature females (\geq 12 mm c.l.), and sexually immature male and female *Bentheogennema burkenroadi* at a sampling location 65 nautical miles (120 km) off Newport, Oreg. (lat. 44°35′N-long. 125°30′W).

Time of		Depth (m)											
year	Size group	0-50	50-100	100-150	150-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900	900-1,000
June 1972	Mature males Mature females						DAY			3 3	4 2	2 3	2 2
Sept. 1972	Immatures Mature males Mature females								1 1 2	5 2	6 6 8	2 4 2	2 1 4
Nov. 1972	Mature males Mature females Immatures			1	1			1	2 2	2 3 1	4 3 1	5	1 1
Mar. 1973	Mature males Mature females Immatures						1		1		13 11 11		
Total number Total volume ir Number/1,000	n 1,000 m³ m³ (day)	103.5 0	149.9 0	1 103.2 0.0097	1 94.7 0.0106	474.7 0	1 497.9 0.0020	1 310.9 0.0032	9 259.6 0.0347	19 132.6 0.1433	41 182.3 0.2249	19 183.3 0.1037	14 162.4 0.0862
						1	VIGHT						
June 1972	Mature males Mature females Immatures	1				1	3 1 2	3		1	1		
Sept. 1972	Mature males Mature females	22		1	1 2	1	1 5	4 2 1	5 2	² 1	2 3	1 1	1 4
Nov. 1972	Mature males Mature females				21	1 4	5 7	2 2 1	1	7 5	3 1 3	1	5 4 1
Mar. 1973	Mature males Mature females Immatures			1	3 1	3 4 2	1 2	1 1	1 1 1	1 2 1	1		·
Total number Total volume in Number/1,000	1,000 m³ m³ (night)	3 111.8 0.0268	530.6 0	2 184.8 0.0108	8 292.8 0.0273	17 251.0 0.0677	30 435.9 0.0688	19 288.6 0.0658	12 261.6 0.0459	20 147.2 0.1359	19 170.7 0.1113	3 132.3 0.0227	15 129.3 0.1160

Twilight 1 h after sunset.

²Twilight 1 h before sunrise.



FIGURE 6.-Day and night length-frequency distributions of male and female *Bentheogennema burkenroadi* n. sp.

night with no progressive drop in concentration with increased depth to 1,000 m (Table 1).

The slight upward movement of this species may be related to its morphology. Vinogradov (1968) considers reduced musculature and a thin integument, which we observed in *Bentheo*gennema burkenroadi, to be a means of achieving buoyancy. Because of weak swimming musculature, they may swim too slowly to keep pace with the upward movement of the stimulating isolume, resulting in broad day and night distributions (Donaldson 1973).

REPRODUCTION

Since penaeid shrimp do not brood their eggs, a description of the breeding cycle must rely on anatomical changes, especially in the development of the ovary and ova. The female reproductive system consists of a bilaterally symmetrical ovary and paired oviducts internally, and externally of a thelycum. Each half of the mature ovary has an anterior lobe angling from the cervical sulcus and almost reaching the base of the eye, and then folding back along itself (Figure 1a). The anterolateral lobe lies over the hepatopancreas extending approximately one-half the way down the body wall. The posterolateral lobe, of such a mature ovary, will have visible distinct ova, measuring up to 240-288 µm crossectional diameter, and will extend ventrally, making a pouchlike structure at the base of each of the fifth pereiopods (Figure 1b). The posterior lobes extend beneath the dorsal abdominal muscle bands.

becoming swollen in the first abdominal segment and then extending on toward the end of the third segment. Females were considered to have reached maturity after attaining a size of 12 mm c.l. and males at a size of 11 mm c.l.

The reproductive cycle, as judged from the sexual condition of the testis and ovary, appears to consist of a 4- to 6-mo spawning season and a 6- to 8-mo resting phase. Based on samples collected in 1972 and 1973, the carapace of females in June is fairly rigid, though the ovaries are not ripe. Some males, from external observation, appear to be ready to release sperm, though most display only partial swelling of the terminal ampoule and vas deferens or lack swelling at all. By fall, females exhibit developing ovaries (two females were in spawning condition), and the carapace is correspondingly rigid. Most males have full, ripe looking testes and dilated terminal ampoules. By the end of November, spawning is in evidence. Most females are mature with readily distinct ova; some mature females have evidently spawned as the thoracic cavity appears empty; the carapace is correspondingly nonrigid, due to the spent ovary which had crowded much of the other organs; others have developing ovaries distended by small diameter ova. All males at this time have ripe testes and dilated terminal ampoules. By February, 50% of all females exhibit signs of spawning activity; the rest have probably spawned because their thoracic cavities appear empty and the carapace nonrigid due to the flaccid ovary. Most males still exhibit ripe testes and enlarged terminal ampoules.

The sex ratio for adult males to females (N = 440), when all tows are included, was: 1:1, 1:1.08, 1:1, 1:1.02, and 1.03:1 for the respective cruises. This approximate 1:1 sex ratio, if it applies to all ages, indicates that there is no selective mortality by sex for this species (Geise 1959).

GROWTH

If spawning occurs from November through February and young (6-7 mm c.l.) enter the population April through June (Figure 7), the intervening egg and larval stages must take 3 to 5 mo. Based on size frequency diagnosis, about 12 additional months are required to reach maturity (11-12 mm c.l.) and another 5 to 6 mo are required before spawning commences Thus the generation time is estimated to be about 2 yr. The largest



FIGURE 7.-Length-frequency histograms of *Bentheogennema* burkenroadi n. sp., from the five cruises (1972-73) off the Oregon coast.

shrimp captured were a 17-mm c.l. male and a 20-mm c.l. female.

Since the mesh size of the net liner was small enough to retain the young (6-7 mm c.l.) and we assume equal chance of capture of young and adults, then adults apparently live more than a year or two after first spawning because the number of adults captured is greater than the number of immature. In fact, the 12- to 15-mm mode must consist of greater than one age class since by itself it exceeds the juveniles in number. This overlap of age classes at >12 mm c.l. indicates that growth slows after maturity is reached.

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